THE EFFECTS OF DISLOCATION OF THE EYE UPON THE ORIENTATION AND EQUILIBRIUM OF THE GOLDFISH (*CARASSIUS AURATUS*).

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It has long been known that the eyeballs of various fishes show different movements during locomotion. It is also established that the body movements have an influence on the movements of the eyes.

Lyon [1] has shown that the dogfish compensates rotation about a dorsoventral axis by moving its eyes in the opposite direction. "The eyes," states Lyon, "sometimes show the same motions when the animal moves voluntarily and normally." "A dogfish, for example, when swimming on its side may keep the upper eye to the ventral, the lower one to the dorsal side of the orbit. Compensatory motions are not, therefore, confined to passive rotation by external means."

Lyon found that these compensatory motions of the eyeballs in fish are practically independent of the sense of light, for they cannot be abolished by blinding (transection of the optic nerves). He also found a causal relationship between the semicircular canals and these eye motions.

The opposite question, whether the eye or visual impressions can influence the body orientation and movements in fish has also been investigated but only in reference to the positive and negative heliotropism. Parker [2] has shown that in an unilluminated field dogfish will swim toward a single light, *i.e.*, they are positively phototropic. Thus the light has a stimulating effect on the progressive movements of the fish and Parker concludes that the retinal image is an important factor in guiding the locomotion of these fishes.

Admitting the fact of positive phototaxis in fishes, there still remains the possibility that in diffused light visual impulses or the fields of vision as a whole may influence the orientation, despite the fact as stated by Lee [3] that "the blinded fish swims normally in all respects."

Numerous experiments by Loeb, Bethe, Bigelow, Lee, Parker, Maxwell, etc., have shown that the labyrinths are concerned with the equilibrium of the fish. The orientation of fish deprived of their labyrinths is very faulty or erratic.

Comparing the striking effects on orientation of labyrinth extirpation with the absence of effects from blinding appears to indicate that the retinal image is not an important factor in equilibrium and orientation in diffused light.

The usual method of studying the influence of the eye on orientation has been that of removal. The difference in the animal's behavior before and after blinding has been interpreted as being due to the removal of the visual function and therefore it is to be considered as representing the normal effect of vision upon orientation and locomotion.

We attempted to approach the problem from a different angle. We tried to investigate the rôle of vision in orientation not by removal but by *dislocation* of the eye, hoping that while the dislocated eye would still perform its visual function, the animal's equilibrium and orientation could be observed and the problem, whether or not the eyes influence orientation, put to a crucial test.

Experimental.

Large goldfish (*Carassius auratus*), eight and twelve inches in length, were chosen for the work because of their availability and especial suitability.[1]

The skull of the goldfish is high, forming a large intracranial space over the brain which permitted the operative work to be done readily. The method chosen was that of dislocation of *one* eye and removing the other. Dislocation was performed by inserting the eye with its nerve and blood supply intact into an artificial orbit placed higher in the skull. This was accomplished in the following way:

A hole about the size of the eye was drilled in the top of the head at a point in the vertical plane of the eyes just to the left of

[1] We acknowledge with pleasure our thanks to Mr. Parker and Mr. Young of the Lincoln Park Zoölogical Gardens, who kindly supplied us with the fish used in this experiment.

the midsaggital line. In the skull and underlying tissue between the left orbit and the drilled hole a narrow channel was cut (including the orbital wall) and thus a communication between the natural and artificial orbit produced. The eyeball was slid along the prepared channel and into the drilled hole, which then served as an artificial orbit. This dislocation can be done very easily and without any force. Neither the eye muscles, nor the nerves of the dislocated eyeball were cut or obviously injured and even the major part of the conjunctiva bulbi and sclerae can be left intact.

The artificial orbit is able to hold the dislocated eye in place indefinitely. At the replacement the dislocated eye showed some healing in the new orbit.

The experiment was successful on two animals. In the third fish a fungus infection on the dislocated eye caused death five days after the operation. To prevent such infections a daily potassium-permanganate (weak solution) bath of the entire fish is necessary.

Immediately following the operation (the first one performed on May 15, 1924) no abnormalities in the animal's behavior were observed. After keeping them under observation for a few days the other eye was removed (May 20, 1924). We were able thus experimentally to produce real cyclopy. These cyclops in their first week behaved exactly like normal blind fish, they swam and oriented themselves quite as before operation. However, after about the tenth day (in our first protocol: June 1, 1924), the animal was observed to tilt the body somewhat to the left. When at rest it assumed a position with its dorsoventral axis several degrees to the left of the vertical. This position was maintained during swimming.

The tilting of the body toward the side in which the eye was dislocated increased day by day, reaching its maximum in about four weeks (in the case of our first animal: June 27, 1924). This maximum tilting was about 45° and was permanent so long as the eye remained in its new orbit.

The gross anatomy of the dislocated eye was quite normal. The media were clear. We observed also some *oscillatory movements* of the dislocated eyes, when we took the fish out of water.

The vision of the fish with dislocated eyes was tested during the period of the last three weeks of the experiment and found to be very good. If a small rod was slowly moved toward the eye the animal quickly turned aside and avoided it constantly.[1] The animal showed in all respects the behavior of a fish in possession of its visual function it avoided all kinds of obstacles. The fishes did not show the phenomenon which Parker described concerning blind fish, *i.e.*, they remain usually near the bottom and swim about in such a way as to be almost continually in contact with some solid surface, as though relying on its sense of touch for its location.

FIG. 1. Goldfish, with the dislocated eye. The other eye removed.

[1] When the animal was near the surface it avoided the rod before it reached the water.

On the 27th of June the dislocated eye was removed from the artificial orbit and slid again along the channel into the original orbit. This operation is also a very easy procedure and can be done without obvious injury of the eye or of the animal.

The animal, as most Anamnia, recovered very slowly from anesthesia and therefore we began our observations on the following day (June 28). The fish was in the normal position at rest and during locomotion. In the several weeks following, the orientation and locomotion were constantly normal, no tilted positions were observed. The other goldfish showed also two weeks after the operation the above described tilting and the tilting reached its maximum six weeks after the dislocation. The results obtained in our second experiment corroborate completely the observations on our first fish with dislocated eye, since in the second animal tilting and the return of vision occurred also synchronously.

At no time during the experiment did the animal show any abnormalities other than the tilting. There were never any evidences of circus movements, etc., which may follow injuries of the midbrain, medulla and labyrinth (Steiner,[4] Loeb,[5] Bethe,[6] Bigelow,[7]).

Discussion.

"A normal fish has a delicate sense of the distance involved in swimming in a straight line. This is shown by the remarkable skill with which he avoids obstacles; in swimming around his aquarium constantly, he strikes his nose directly against the side of the tank comparatively rarely. This is not so with a fish deprived of all his otoliths or with all his macular nerves severed. Such fish seems to have little idea of the extent of a forward swim. He is often restless and frequently alters the direction of his progression" (Lee,[3]). In his experiments Lee did not include the positive side of the rôle of vision in the orientation and equilibrium of the fish. Lee says, "When left to himself, the blinded fish swims normally in all respects, moving gracefully, easily, and without timidity, and shooting and diving like an uninjured fish."

The first question which confronts us is, of course, the cause and mechanism of the tilting following the eye dislocation. There can be little doubt that the tilting is directly due to the dislocation of the organ for light perception. We avoided injury to the brain and otic capsule and the immediate post-operative behavior of the fish proves that there were no lesions of those organs.

Any continuous tilting of the fish is called a "forced position" by Loeb. Loeb discriminates in one of his earliest papers between two different types of forced responses: "forced movements and forced position." "Wir sprechen von Zwangsbewegungen, wenn die Tiere sich kontinuirlich oder sehr häufig in Bahnen bewegen, die von denen eines normalen Thieres unter den gleichen Umständen in einem bestimmten einfachen Sinne abweichen." And on the other hand: "Wir bezeichnen als Zwangslagen die Abweichungen von der normalen Orientierung gegen den Schwerpunkt der Erde."

According to Loeb the forced *positions* are due to geotropism. Moreover, he refers to the fishes as one of the clearest instances of such phenomena. The normal *position* of fishes in swimming or at rest is also, according to Loeb, a geotropic phenomenon. "Versuchen wir es einen solchen Fisch gewaltsam auf den Rücken zu legen, so widerstrebt er und bringt, so bald wir ihn wieder frei lassen, sich wieder in seine gewohnte Orientierung zurück."

Even the position of the eyes are influenced by the gravitation in the fish. "Bringen wir den Kopf eines Fisches gewaltsam in eine andere als die ihm zukommende Orientierung gegen die Schwerkraft der Erde, so gehen die Augen völlig oder theilweise in die alte Orientierung zurück. . . . Das Licht hat mit diesen Erscheinungen nichts zu schaffen, sie treten auch, wie bekannt, im Dunkeln und bei völlig Erblindeten ein." (Loeb [5]). As Loeb points out the orientation of the fish in relation to gravity takes place by means of the otolith apparatus, as first demonstrated by Mach and Breuer. Loeb cut (in *Scyllium canicula*) the right VIIIth nerve. He saw forced circus movements to the side of the lesion, forced tilting toward the side of the lesion, pleurothotonus, and compensatory positions of the eyeball and fins.

Bethe does not deny the static function of the labyrinth, but he states that the geotropism of the Elasmobranches is not essentially changed by the removal of *one* labyrinth. He failed to observe in many animals the forced positions as after-effects of unilateral labyrinth-extirpation, but admits that forced movements and forced positions of the eyeballs and fins can often be seen in such animals. He says that the unbalanced tonus and innervation of the trunk, eye and fin muscles (Ewald) can explain satisfactorily these forced motions. But he admits that this tonus factor is also influenced by the geotropic function of the labyrinth.

Although different authors describe somewhat differently the after-effects of labyrinth extirpation (this may be due to difference in technique, injury of other cranial organs, etc.), all seem to agree on the point that the *geotropic* function of the labyrinths is responsible for normal orientation and equilibrium.

No other factor has been considered to play an important part in this behavior. Dogfish in which both labyrinths were removed as observed by Maxwell (8), could hardly be seen to differ from that of the normal fish except when greatly excited. They swim quietly around or settle on the bottom in normal position. Maxwell raised the question whether the orientation of labyrinthless fish is due to retinal stimuli, but his experimental results showed to him that visual impulses did not play a rôle in the orientation of his operated fish. When he covered each eye with a large patch of heavy, black, rubber cloth, the animal swam about with good orientation and never came to rest on the bottom in an abnormal position. This goes to show that in nature chronic or permanent tilting of the body of the fish occurs only from unilateral injury of the labyrinths and never from eye injuries. When both labyrinths are removed there remains no mechanism on which gravity can act in the way to induce orientation, according to Loeb.

In our fish the labyrinths were normal and the otoliths should have taken care of the normal position in swimming or at rest. Nevertheless the tilting of the body took place, as described. Evidently the influence of the labyrinth was modified by a new factor of vision. This factor is probably the influence *of the visual field* on the orientation mechanism.

As long as the vision was impaired by the trauma of the operation, no tilting of the body was noticed. The question is, whether this tilting is a phototropic reaction, a "forced" reaction or due to attempts of the animal to keep its usual visual field. Maxwell admits the possibility of such a mechanism, of course in a different type of experiment: "When the dogfish is rotated around any one of these axes the eyes move as if to retain their original position in space, or to preserve the original visual field."

We think that the tilting is due to so-called "voluntary" motor attempts of the fish to regain or retain the *usual* visual field.

Heliotropic reactions involve different mechanism in fish than in the invertebrates, for Parker has shown that the dogfish, when only one optic nerve is cut, never moves in circles.

Since in the tank, where the fish lived, there were diffused light conditions, there was no single source of light that could act as a phototropic stimulus. Interpretation of the tilting as a *simple* phototropic response seems therefore excluded.

The tilting at 45° was the optimal condition for the animals to *see* the walls of the aquarium and most of the environment with which he can come in contact and our results indicate that the tilting is a quick reaction of the organism as a whole.[1]

Summary.

1. The dislocation of one eye into the top of the head and the removal of the other eye produce a tilting of the whole body with its dorsoventral axis 45° to the side of the vertical. The reposition of the dislocated eye into its original orbit changes the orientation and equilibrium of the fish immediately, it regains its normal position in swimming and at rest.

2. The tilting is probably due to the attempts of the animal to keep its usual visual field.

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[1] If so, then the fish placed in the dark or by cutting its only optic nerve should regain its normal position. We contemplate to investigate this and related problems in further experiments.